

# VARIATIONS IN THE LARVAL STAGES OF A DECAPOD CRUSTACEAN, PLEURONCODES PLANIPES STIMPSON (GALATHEIDAE)<sup>1</sup>

CARL M. BOYD<sup>2</sup> AND MARTIN W. JOHNSON

*Scripps Institution of Oceanography, La Jolla, California*

During the last decade extensive literature has been accumulating on the larval development of several species of decapod Crustacea. Costlow, Bookhout and Monroe (1960) have reared several species of Brachyura. Rees (1959) has reared *Emerita talpoida*, Coffin (1958) successfully raised species of pagurids, and Broad (1957a and 1957b) raised two species of Macrura (*Palaemonetes*). The Brachyura, with rare exceptions, all pass through a constant number of molts, though duration of time spent in the various larval stages is influenced by temperature and salinity. Broad (1957b) found that the number of molts passed through, and the duration of the larval stages, in *Palaemonetes* were influenced by type of food available to the larvae. Among the Anomura the picture is less clear. Johnson and Lewis (1942), in a study of larvae of *Emerita analoga* from the plankton, described the morphology of several discrete stages, and reported several specimens which appeared intermediate between stage III and stage IV; the authors assumed that the intermediate forms indicated variation in the molting sequence. When Rees reared the larvae of *E. talpoida*, he noted that some went through a stage that was deleted by others. The precise molting history of individual larvae in many of the studies has been obscured in laboratory studies by the practice of rearing several larvae in the same container. In plankton studies the observers are generally unable to discern what degree of morphological variation occurs within the confines of the same larval stage.

In 1960 one of us (Boyd) described and figured five larval stages of *P. planipes*, based on specimens taken from the plankton in neritic waters off southern Baja California. The five stages were morphologically discrete, and it was assumed that each stage was passed through in a single molt. Since then the larvae have been reared through the larval stages, the immature phase, and on to maturity, a total span of about a year. Laboratory data support the validity of the five stages described and add a great deal of information concerning the larval development.

*Pleuroncodes planipes* is an anomuran galatheid crustacean, about 9 to 11 cm. long as adults, and resembling a small homarid lobster. These red crabs, as they are commonly called, exist both as pelagic and benthic animals. The crabs occur along the coasts of California and Baja California, over a range from 16° N. to 37° N. and have a distribution which is typically neritic in the pelagic phase. Distribution, growth rates and notes on the biology of the adults and post-larval crabs are presented elsewhere (Boyd, 1963).

<sup>1</sup> Contribution from the Scripps Institution of Oceanography, University of California, San Diego.

<sup>2</sup> Present address: Institute of Oceanography, Dalhousie University, Halifax, Nova Scotia.

## REPRODUCTION

Adult *Pleuroncodes planipes* females carry their eggs attached to their pleopods in the same manner as brachyuran and other anomuran crabs. Specimens in the laboratory bred and laid eggs readily; the eggs produced were carried from 6 to 22 days (generally about 14 days). During that time the eggs changed from a golden color to a dark amber, as the eyes of the embryos developed. All the larvae hatched out as swimming Stage I zoeae, and once hatching began, all the eggs carried by

TABLE I

*Numbers and ratios of post-larval male and female Pleuroncodes planipes caught in the monthly CalCOFI plankton samples, from December, 1958, to August, 1960. The number of these females which were carrying eggs is also given.*

Cruise	Number & % males	Number & % females	Number & % of those females gravid	Month
5812	13 (54)	12 (46)	0 (0)	December
5901	293 (55)	241 (45)	27 (11)	January
5902	169 (51)	161 (49)	58 (36)	February
5903	16 (40)	24 (60)	0 (0)	March
5904	186 (58)	133 (42)	0 (0)	April
5905	111 (51)	106 (49)	0 (0)	May
5906	89 (52)	83 (48)	0 (0)	June
5907	193 (51)	186 (49)	0 (0)	July
5908	400 (60)	291 (40)	0 (0)	August
5909	46 (52)	42 (48)	0 (0)	September
5910	140 (55)	113 (45)	0 (0)	October
5911	3 (100)	0 (0)	0 (0)	November
5912	0 (0)	2 (100)	1 (50)	December
6001	199 (59)	141 (41)	41 (29)	January
6002	168 (61)	106 (39)	59 (56)	February
6003	324 (49)	334 (51)	133 (40)	March
6004	413 (55)	341 (45)	2 (.6)	April
6005	180 (46)	208 (54)	0 (0)	May
6006	71 (52)	66 (48)	0 (0)	June
6007	106 (57)	79 (43)	0 (0)	July
6008	87 (51)	84 (49)	0 (0)	August
Total	3207	2753		

a female hatched within about 12 hours. Females carry up to 3650 eggs (the largest number counted in the study); larger females tend to have the greater number of eggs. Females kept isolated from males occasionally produced eggs, but these were invariably sterile, and were sloughed off from the pleopods within a few days. Records of individual females in the laboratory indicate that each female usually had two, and rarely three, broods of eggs per season. Sexual maturity, as denoted by the ability of the females to produce eggs, was attained at a size of 14–15 mm. standard carapace length. Females of that size are about 12 months old.

In the laboratory the egg-bearing season lasted from November through April, with the peak in February. Table I shows that the egg-bearing season in the field followed a similar pattern.

The numbers of males and females caught in the plankton tows of the California Cooperative Oceanic Fisheries Investigations between December, 1958, and August, 1960, differed significantly from 50/50 at the 0.01 level, as tested by the signed ranks test, two-tailed. The average percentage observed was 53.85% males and 46.15% females. The reasons for this departure from the 50/50 sex ratio are not known, but the departure may result from one or more of the following: (1) more males may be hatched than females, (2) females may have a lower survival rate than males, or (3) the plankton nets may not sample males and females with equal effectiveness.

#### METHODS

The rearing techniques used in this study are similar to those described by Broad, Coffin, Costlow *et al.*, and Rees. They involve the use of antibiotics to reduce the numbers of contaminating bacteria in the larval cultures, and also the use of *Artemia* nauplii for larval food. Freshly hatched larvae of *P. planipes*, taken from adult females kept in the laboratory, were pipetted into containers filled with sea water taken from the end of the pier of the Scripps Institution of Oceanography, La Jolla, California, where this work was done. The water had been filtered through glass wool to remove detritus and larger animals that might prey upon the larvae.

Experiment 1; started 19 February, 1960; duration 74 days. Two hundred freshly hatched larvae were placed, 10 per container, in 20 one-liter styrene plastic containers, each holding 500 ml. of water with antibiotics. The antibiotics used were (1) 50 mg./liter streptomycin (trade name "Combistrep" by Pfizer; dihydrostreptomycin and streptomycin sulfate; powder), and (2) 50 mg./liter penicillin (penicillin G by Abbott, pill form, buffered with  $\text{CaCO}_3$ , 928 units per mg., ground to a powder before use). This penicillin was used because earlier experiments indicated that the more readily available penicillin (a mix of 75% procaine penicillin and 25% penicillin G) was toxic to crab larvae. The containers were placed in trays of flowing sea water, which held them at temperatures ranging from 15° C. in February to 18° C. in June. Larvae were transferred to fresh sea water twice each week, and freshly hatched *Artemia* nauplii were added at that time. In the process of transferring the larvae into the fresh medium, each was drawn up into a 2-mm. bore glass pipette and examined through the pipette under a low power dissecting microscope to determine its stage.

Experiment 2; started 1 March, 1960; duration 74 days. One hundred larvae, 10 in each of 10 containers, were treated similarly to the larvae in Experiment 1, except that the penicillin was omitted; streptomycin was used in concentrations of 50 mg./liter; temperatures ranged from 15° to 18° C.

Experiment 3; started 12 April, 1960; duration 108 days. Ninety-three larvae were kept individually in plastic containers in 50 ml. sea water; 50 mg./liter streptomycin were added. Temperature, 16° to 19° C. Larvae were fed, transferred into new medium, and examined as in the preceding experiments. The containers were checked daily for exuviae and these, if present, were removed and preserved in glycerine on slides.

## RESULTS OF EXPERIMENTS 1, 2, AND 3

The experiments proved that the larvae could be reared through all larval stages in the laboratory, and gave information concerning the total duration of the larval phase. The data are summarized in Table II.

Each of the seven larvae to complete the larval phase in Experiment 1, and one of the 56 in Experiment 2 passed through a new stage, VI. This stage has never been seen in a search of hundreds of larval specimens from the plankton. It was similar in morphology to Stage V, but was larger and characterized by a tuft of plumose setae on each of the pleopods. It is probable that it was an artifact of treatment, and its presence was due either to the penicillin or to the  $\text{CaCO}_3$  buffer in the pills used, for other conditions were similar. As later experiments involving mixtures of non-buffered penicillin and streptomycin did not give Stage VI larvae, it is possible that the carbonate was the cause.

It was noted in the first two experiments that Stage IV had a longer duration than the other stages. Modal values in Experiment 2 were: Stage I, 9 days; Stage II, 8 days; Stage III, 8 days; Stage IV, 25 days; Stage V, 12 days. The mean durations could not be calculated because larvae were followed as a popula-

TABLE II  
*Duration and survival of larvae in Experiments 1, 2 and 3*

Exp.	Shortest duration of larval phase	Longest duration of larval phase	Average	Survival through larval phase
1	54 days	68 days	61 days	7/200 = 3.5%
2	53 days	74 days	64 days	56/100 = 56%
3	71 days	110 days	87 days	15/93 = 16%

tion, and not as individuals. It was suspected that Stage IV consisted of at least two sub-stages, but the exact number of sub-stages or the morphological differences between them could not be determined because the history of individual specimens could not be followed. Experiment 3 was set up to make it possible to follow individual specimens through the larval stages.

Although the volume of water per larva was identical (50 ml.) in each of the three experiments, and other conditions were the same in Experiments 2 and 3, the duration of the larval phase was longer in Experiment 3 than in either 1 or 2 (*cf.* data presented above). The three average values cannot be compared in the usual manner because the duration of the larval period in Experiments 1 and 2 is not known for individual larvae, and a variance cannot be calculated. A comparison of the ranges, however, indicates that the values for Experiment 3 differ significantly (at better than the 0.05 level) from the values for Experiments 1 and 2, but that the latter do not differ between themselves. The slightly greater temperature of Experiment 3, if it had any effect, should have caused a shortening of the larval period (see below). The only parameter in the three experiments which was known to be very different was the isolation of individual larvae in Experiment 3 versus their group rearing in Experiments 1 and 2. This difference had two components: the larvae had less total water in which to swim, though the volume

TABLE III

*The percentage of larvae passing through each sub-stage of Stage IV  
(Experiment 3)*

IVa = 100%	IVe = 82%
IVb = 100%	IVf = 65%
IVc = 100%	IVg = 59%
IVd = 100%	IVh = 29%
	IVi = 2% (died before reaching Stage V)

of water per larva was identical, and they were not in association with other larvae. Either may have prolonged the larval phase in Experiment 3.

By following the molting sequence of individual larvae it became evident that the number of molts passed through before a larva completed the larval phase varied between larvae. The morphology of Stages I, II, and III in the laboratory was as described in 1960, based on larvae taken from plankton collections. Each of these stages was completed after a single molt. Stage IV, however, was divided into a series of what can be called sub-stages, each separated by a molt, but all morphologically within the general description of Stage IV. The larva increased in size through the sequence of sub-stages, and the number of setae on some of the appendages (*e.g.*, uropods, antennal scales) increased, but the differences between the various sub-stages of the complex were so inconsistent that a sub-stage could be identified with certainty only by knowing how many molts the larva had passed through. The number of sub-stages within the Stage IV complex varied from four to nine. The percentage of larvae passing through each sub-stage is given in Table III.

The mean duration of each of the larval stages and the 95% confidence limits of the sample, the cumulative elapsed time to the end of each particular stage ( $\Sigma$ ), the number of larvae completing each stage ( $N$ ), and the instantaneous death rate based on  $N_t = N_0 e^{-dt}$  are given in Table IV.

TABLE IV

*The mean duration of each larval phase and the 95% confidence limits of the sample.  
The cumulative elapsed time to the end of each particular stage ( $\Sigma$ ), and the  
number of larvae completing each stage ( $N$ )*

Stage	Mean duration and 95% limits (days)	$\Sigma$ (days)	$N$	Instantaneous death rate (days)
I	11.9 $\pm$ 5.7	11.9	46	0.059
II	8.0 $\pm$ 4.5	19.0	45	0.003
III	7.4 $\pm$ 5.7	27.3	41	0.013
IVa	6.9 $\pm$ 3.8	34.2	39	0.007
IVb	6.7 $\pm$ 5.9	40.9	36	0.012
IVc	7.4 $\pm$ 4.3	48.3	32	0.016
IVd	8.8 $\pm$ 5.4	57.1	28	0.015
IVe	8.7 $\pm$ 4.4	65.8	22	} 0.016
IVf	11.1 $\pm$ 6.6	76.9	18	
IVg	9.8 $\pm$ 4.7	86.7	16	
IVh	10.0 $\pm$ 4.0	96.7	8	
V	13.7 $\pm$ 6.6	86.9	15	0.000

The instantaneous death rate cannot be tabulated for individual stages subsequent to sub-stage IVd, for the deletion of stages is confused with mortality in the data analysis. It is evident from the table that the highest death rate occurred in the first stage, and mortality after that was essentially equal one stage to the next.

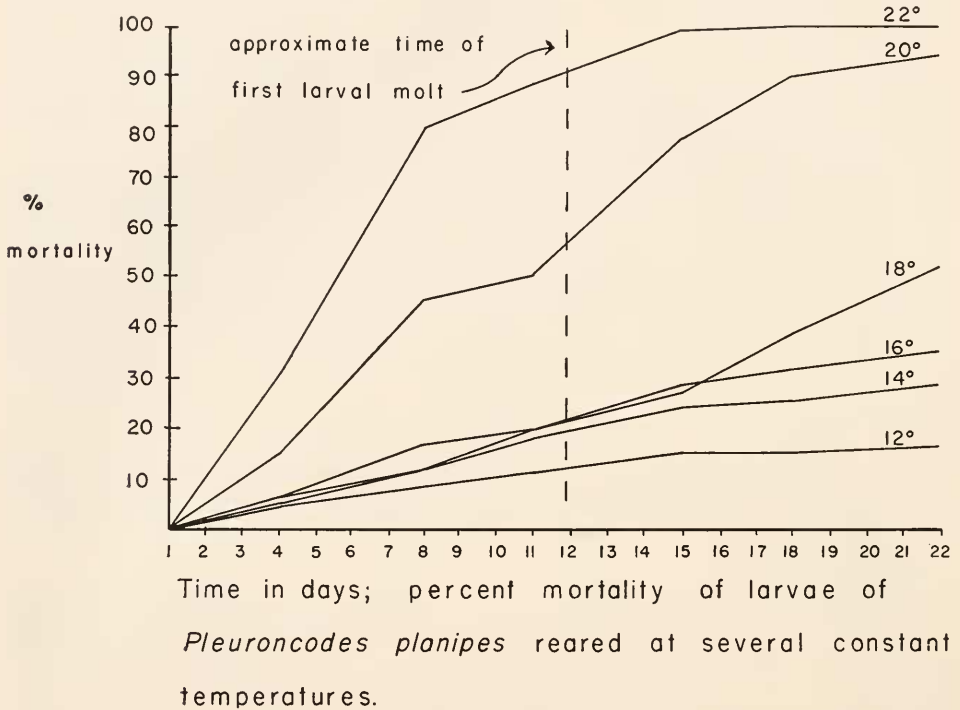


FIGURE 1. Mortality of larvae of *Pleuroncodes planipes* reared in the laboratory at several constant temperatures.

#### EXPERIMENT 4

##### METHODS

This experiment started April 25, 1960; duration 163 days. A device was designed and constructed which maintained larval cultures at six constant temperatures. The temperatures selected were 12°, 14°, 16°, 18°, 20°, and 22° C. The two extreme temperatures selected are approximately the surface temperatures of, respectively, the northern and southern ends of the distributional range of the adults in the spring months (the breeding season). Larvae were placed in sea water containing 50 mg./liter penicillin (Pfizer, penicillin G, potassium; 1585 units/mg. powder) and 50 mg./liter streptomycin (Combistrep, by Pfizer). Larvae were transferred into fresh sea water twice each week, and at that time were staged under the microscope and fed as in the previous experiments. The larvae were kept in styrene containers, each containing 18 compartments which measured 4.5 × 5.0 × 3.8 cm. deep and held 50 ml. of sea water. Six containers were used at

each temperature; initially, two larvae were placed in each compartment, giving 216 larvae at each temperature, or a total of 1296 larvae. All of these larvae were obtained from the same female over a period of about 12 hours. The extra larva was placed in each compartment because Experiment 3 had shown that mortality was highest in the first few days. After 22 days the extra larvae in the 12°, 14°, and 16° cultures were discarded, leaving individual larvae (108 total) in the compartments; mortality had been higher at the higher temperatures, so that only 101 larvae remained at 18°, 16 larvae at 20°; and none at 22°.

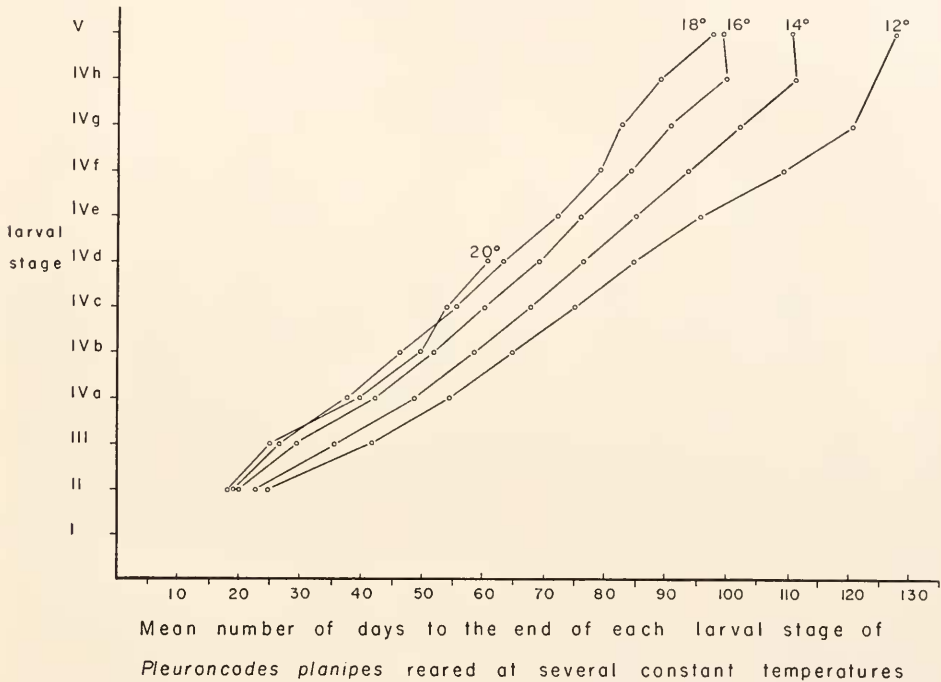


FIGURE 2. Rates of development of larvae of *Pleuroncodes planipes* reared in the laboratory at several constant temperatures.

RESULTS OF EXPERIMENT 4

The mortality data for the first 22 days are shown in Figure 1. The estimated instantaneous death rates through Stage 1 (0-11.9 days) are: 12°, 0.011; 14°, 0.018; 16°, 0.020; 18°, 0.020; 20°, 0.074; 22°, 0.192. No larvae completed the larval phase in either the 20° or 22° cultures; these temperatures may therefore be regarded as lethal in this experiment.

Within certain limits larval development should be faster at high temperatures; Figure 2 shows that this is true for *P. planipes*, at least over the range from 12° to 18° C. No data are available for the duration of Stage I because at the time the larvae were in that stage they were not kept individually. In Figure 2 it will be noted that the cumulative mean number of days to the end of sub-stage IVh

is greater than the developmental time to the end of Stage V for the 14° and 16° cultures. This is because many larvae omitted one or more of the later Stage IV sub-stages and passed directly to Stage V, thereby shortening their larval duration. The trend of the 20° line is probably correct but it is based on too few individuals

TABLE V

*Mean duration of stages of P. planipes larvae reared at several temperatures. These durations are cumulatively summed and presented under the heading  $\Sigma$ . The number of larvae passing through each stage is presented under N.*

12°				14°			
Stage	Mean duration and 95% limits	$\Sigma$	N	Stage	Mean duration and 95% limits	$\Sigma$	N
II		24.7		II		22.3	
III	16.9 ± 7.0	41.6	84	III	13.2 ± 8.1	35.5	61
IVa	12.8 ± 5.4	54.4	71	IVa	12.6 ± 9.6	48.1	52
IVb	10.7 ± 5.8	65.1	68	IVb	9.9 ± 5.9	58.0	45
IVc	10.4 ± 6.7	75.8	63	IVc	9.5 ± 6.8	67.5	42
IVd	9.1 ± 5.1	84.6	60	IVd	9.3 ± 5.2	76.8	37
IVe	11.7 ± 5.1	96.3	56	IVe	7.2 ± 4.0	84.0	35
IVf	12.4 ± 7.0	108.7	50	IVf	9.1 ± 3.8	93.1	33
IVg	12.0 ± 6.7	120.7	13	IVg	8.9 ± 3.0	102.0	15
IVh				IVh	9.0 ± 5.7	111.0	2
V	17.7 ± 7.9	127.5	50	V	13.2 ± 4.7	110.9	31
16°				18°			
Stage	Mean duration and 95% limits	$\Sigma$	N	Stage	Mean duration and 95% limits	$\Sigma$	N
II		19.7		II		19.0	
III	9.6 ± 7.1	29.3	57	III	7.8 ± 6.0	26.8	33
IVa	12.8 ± 6.6	42.1	51	IVa	10.6 ± 6.5	37.4	12
IVb	10.0 ± 6.9	52.1	43	IVb	8.8 ± 4.8	46.8	9
IVc	8.8 ± 7.0	60.9	37	IVc	9.2 ± 4.2	55.4	5
IVd	8.1 ± 5.8	69.0	34	IVd	7.6 ± 2.8	63.0	5
IVe	7.6 ± 4.7	76.6	32	IVe	9.0 ± 3.6	72.0	4
IVf	7.4 ± 5.9	84.0	28	IVf	6.8 ± 1.1	78.8	4
IVg	7.2 ± 4.3	91.2	17	IVg	4.0	82.8	2
IVh	8.5 ± 4.3	99.7	2	IVh	6.0	88.8	1
V	10.6 ± 3.3	98.4	30	V	11.7 ± 1.7	97.7	3
20°							
Stage	Mean duration and 95% limits	$\Sigma$	N				
II		18.0					
III	7.0	25.0	3				
IVa	14.5 ± 3.5	39.5	2				
IVb	10.0	49.5	1				
IVc	4.0	53.5	1				
IVd	7.0	60.5	1				



TABLE VI

- A. The number of larvae which molted directly to Stage V from each sub-stage, thereby omitting later sub-stages
- B. The above data are expressed as the per cent of larvae which completed a particular sub-stage before becoming Stage V larvae

	12°	14°	16°	18°
IVe	3	1	3	0
IVf	37	17	11	1
IVg	13	13	15	1
IVh	0	2	2	1
V	53	33	31	3
IVe	100	100	100	100
IVf	94	97	90	100
IVg	24	45	55	67
IVh	0	6	6	33

to be very accurate; at the end of Stage III only three larvae were alive in the 20° culture. The mean duration of each stage (with the 95% confidence limits of the sample) is shown in Table V. The values are cumulatively summed to give the average total number of days elapsed to the end of each stage.

A  $Q_{10}$  value for the rate of larval development of *P. planipes* can be calculated on the basis of the mean number of days of life to the end of the larval phase. The first three values, 128, 111, and 98 (for 12°, 14°, and 16°, respectively), give an average  $Q_{10}$  of 1.95. The fourth value, for 18° (98), when compared with the 12° value gives a  $Q_{10}$  of 1.6. This figure is based on only three larvae at 18°, and is suspect; the correct value is probably about 1.9.

The number of sub-stages passed through in Stage IV varied from larva to larva in this experiment as it did in Experiment 3.

From Table V it can be seen that no larvae in the 12° culture went into sub-stage IVh; at other temperatures some larvae went through this sub-stage on their way to Stage V. The number of larvae which molted directly to Stage V from each sub-stage, and thereby omitted later sub-stages, is tabulated in Table VI (A). These data may be expressed as the per cent of larvae which completed a particular sub-stage before becoming Stage V larvae (Table VI (B)). A Friedman analysis of variance can be applied to the last three rows of figures in Table VI (B). This tests whether the columns of numbers come from the same population, and yields, in this case, a probability of 0.075. If one regards this value as significant, the data are evidence of a trend indicating that at higher temperatures larvae pass through more sub-stages than they do at lower temperatures. This is in spite of the fact that the total larval span in time is shorter at higher temperatures.

#### DISCUSSION

Perhaps the most interesting observation to result from the culturing of larvae of *P. planipes* in the laboratory is that Stage IV is divided into sub-stages, and

that the number of these sub-stages may vary. The data indicate that the number of sub-stages which a larva passes through may be influenced by the temperature of the environment, with higher temperatures producing more sub-stages before the molt to Stage V; that within limits the rate of larval development shows a  $Q_{10}$  close to 2; and that higher temperatures cause a higher death rate.

Environmental factors other than temperature affect the duration of the larval stages. For example, temperatures were the same in Experiments 2 and 3, but there was a difference in the mean larval duration. The only known differences in conditions were the size of the rearing container and the presence of other larvae in the same container. Gurney (1942) conjectured that data concerning the life-histories of laboratory-reared larvae might prove misleading when applied to larvae in the ocean. In view of the demonstrated effects of various small changes of conditions on the molting sequence and developmental duration of laboratory-reared larvae, it is quite possible that their life-histories may be inapplicable to larvae in the field. The matter is further discussed by Rees (1959). In the case of *P. planipes* larvae, however, all of the stages, except Stage VI, seen in the laboratory, including evidence for a complex of Stage IV sub-stages, can be found in larvae from the plankton. The number and detailed morphology of the Stage IV sub-stages which larvae pass through in the ocean may well differ from the number passed through by larvae in laboratory experiments, and the number of sub-stages may even vary from one part of the ocean or one season of the year to another.

The irregularities in the number of molts in the larval phase shown by *P. planipes* may be found in other anomuran crabs. Sub-stages, however, are difficult to detect in morphological studies of larvae taken from plankton collections. Johnson and Lewis (1942) found a "lower Stage IV" in the larval stages of *Emerita analoga*, based on larvae from the plankton. This lower stage is best interpreted as a sub-stage and is an indication that sub-stages occur naturally in the field. Rees (1959) noted that larvae of *Emerita talpoida* reared in the laboratory may pass through either 6 or 7 molts before becoming megalops. Similar results were noted in laboratory-reared larvae of *E. analoga* by Dr. Ian Efford (unpublished results, personal communication). A. Provenzano (personal communication) has observed a varying number of molts in larvae of some pagurid crabs from Florida cultured by him. Costlow (personal communication), however, has observed variation in the number of larval molts in only two species of Brachyura out of a total of about 20 species—both Portunidae; variation occurred only occasionally and resulted in a form with reduced viability which only rarely developed to the megalops stage. Broad (1957a, 1957b) found that the number of larval molts varied in *Palaemonetes pugio*, a decapod macruran, depending on the type of food given the larvae.

Stage VI, which appeared in Experiment 1, has never been found in the plankton and appears to be the result of laboratory rearing conditions. It is possible that it occurs in nature under certain conditions. Its existence would certainly support Gurney's contention that laboratory conditions produce aberrant larval forms. Kurata (1960) observed what may be a similar phenomenon in the advanced stages of two lithodid crabs (*Paralithodes camtschatica* and *P. brevipes*) reared in the laboratory. These stages were intermediate between the usual last larval stage and the glaucothoe.

The temperatures in Experiment 4 (12° to 22° C.) were selected because these are approximately the surface temperatures at the northern and southern ends of the crab's distribution in the adult phase. The few data available (unpublished) indicate that the larval distribution is similar to the adult distribution, with the greatest concentrations occurring along the western coast of southern Baja California. In that area winter temperatures may commonly be as high as 20° at the surface. Larvae at that temperature in the laboratory had a higher mortality rate than did those at lower temperatures. Possibly, larvae in the latitude of southern Baja California do not live at the surface but rather below the surface at a more optimal temperature. The winter breeding season may be correlated with higher larval survival in the laboratory at colder temperatures.

Because problems encountered by the larvae of many polychaetes and the decapod crustaceans are similar, in that they must transform from a pelagic phase to a benthic phase, it is tempting to speculate that decapod crustacean larvae such as those of *P. planipes* may respond to environmental parameters in a way similar to that demonstrated by Wilson for various polychaete larvae (*cf.* Wilson, 1952). He has shown that polychaete larvae are influenced by the nature of certain substrates so that they end the pelagic phase and become benthic. The presence of other substrates tended to prolong the larval phase. Experiments similar to Wilson's have not yet been performed on larval decapods, however, presumably because of the difficulties inherent in rearing them.

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#### SUMMARY

1. The young of *Pleuroncodes planipes* pass through a series of five morphologically discrete zocal larval stages after hatching, and, except in Stage IV, the larvae change from one stage to the next by a single molt. Larvae in Stage IV may molt from four to eight times without greatly altering their basic morphology. There is evidence from laboratory culturing that the number of these sub-stages may be influenced by the temperature at which the larvae develop, with higher temperatures causing more sub-stages.

2. The duration of the larval phase is influenced by the temperature at which the larvae are reared, and the rate of development follows a  $Q_{10}$  of about 1.9. The larval duration is also influenced by rearing conditions other than temperature, for the size of the larval rearing container or the presence of other larvae in the container has also been shown to influence the duration of the larval phase.

3. A larval stage was seen in the laboratory which has not been found in nature, and it is probable that the stage was an artifact of laboratory culturing conditions.

4. It may be generalized that variation in the number of larval molts is widespread in the Anomura; variation does not commonly occur in brachyuran Crustacea.

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